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Middens of the earthworm *Lumbricus terrestris* (Lumbricidae): microhabitats for micro- and mesofauna in forest soil

Mark Maraun[1], Jörn Alphei[2], Michael Bonkowski[2], Romuald Buryn[2], Sonja Migge[3], Maren Peter[2], Matthias Schaefer[2], Stefan Scheu[1]

[1] Technische Universität Darmstadt, Institut für Zoologie, Schnittspahnstraße 3, 64287 Darmstadt, Germany
[2] Universität Göttingen, Institut für Zoologie und Anthropologie, Abteilung Ökologie, Berliner Straße 28, 37073 Göttingen, Germany
[3] University of Calgary, Department of Biological Sciences, 2500 University Drive NW, Calgary, Alberta T2N 1N4, Canada

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Summary. In September 1994 microflora (microbial biomass, basal respiration, specific respiration), microfauna (Nematoda) and mesofauna (Gamasina, Uropodina, Collembola, Oribatida) in middens of the deep-burrowing earthworm *Lumbricus terrestris* and in the surrounding (non-midden) soil were investigated in a beechwood (*Fagus sylvatica*) on limestone. In middens C and N content, C/N ratio, microbial biomass, basal respiration and specific respiration were significantly higher than in non-midden soil. The abundance of Gamasina and Uropodina (mainly *Dinychus perforatus* and *Trachytes aegrota*) and biomass of Nematoda (especially that of bacterial feeders and omnivores) were higher in the middens whereas most oribatid mite taxa (Brachychthonidae, Oppiidae, Poronota) preferred the non-midden soil. Total density of Collembola differed little between midden and non-midden soil. However, three species of Isotomidae (*Isotoma violacea, Folsomia quadrioculata* and *F. manolachei*), *Onychiurus furcifer* and *Stenaphorurella denisi* were more abundant in middens, whereas *Lepidocyrtus lanuginosus* was more abundant in non-midden soil. Generally, even closely related species or other taxa responded differently to the presence of middens as indicated by principal component analysis (PCA). It is concluded that middens of *L. terrestris* contribute to the patchiness and heterogeneity of the forest floor and serve as important microhabitats for some soil animals. Middens are – at least temporarily – preferred habitats or refuges for several groups of soil animal species while others avoid middens as habitats or are detrimentally affected by environmental conditions in middens. The structural and temporal dynamics of this microhabitat may partly be responsible for the coexistence of large numbers of species, e.g. allowing various prey species (Nematoda, Collembola) to reach high densities. It is concluded that the increased biomass of bacterial feeding nematodes and euryoecious Collembola was caused by an increased microbial biomass in the middens and that predacious Gamasina and Uropodina benefited from this increased prey density but were unable to effectively control prey populations. The flourishing of most animal taxa in earthworm middens where the amount of food was higher than in non-midden soil supports the view that bottom-up forces dominate in decomposer communities.

Key words: Earthworm middens, Gamasina, Uropodina, Collembola, Oribatida, Nematoda, microhabitat, beechwood

Correspondence to: Mark Maraun, email maraun@bio.tu-darmstadt.de

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Introduction

Earthworms are important ecosystem engineers, particularly in forest soils (Jones et al. 1994; Lavelle 1997). Through burrowing, casting and mixing of litter and soil (bioturbation) they influence aggregate stability, water flow, nutrient mineralization, microbial activity and plant growth (Lee 1985; Edwards & Bohlen 1996). In base-rich forest ecosystems their activities dominate the formation of the soil structure. In contrast to process oriented studies there are only few studies investigating the effect of earthworm activities on other soil animals (Brown 1995; McLean & Parkinson 1998; Parkinson & McLean 1998). Anecic earthworms like *Lumbricus terrestris* produce high numbers of casts on the soil surface. These casts are intensively mixed with decomposing litter materials forming conspicuous structures termed middens which contribute to the heterogeneity and patchiness of the forest floor. It has been speculated that earthworm middens might be an important microhabitat for soil animals because they offer spatial and temporal refuges for the soil micro- and mesofauna allowing coexistence of high numbers of species in close proximity (Anderson 1975; Szlavecz 1985; Hamilton & Sillman 1989; Giller 1996).

It is known that physical, chemical and microbial properties of earthworm casts differ considerably from that of soil. Contents of carbon, nitrogen, phosphorus, and soil moisture in cast materials are higher than in soil (Graff 1970; Sharpley & Syers 1976; Syers et al. 1979). Microorganisms are assumed to flourish in earthworm casts (Parle 1963; Domsch & Banse 1972; Tiunov & Scheu, in press) and may serve as a food resource for other soil animals.

In a series of papers the influence of Lumbricidae on decomposition processes in a hornbeam-oak mixed forest in Hungary was reported (Zicsi 1975; Zicsi & Pobozsny 1977; Zicsi et al. 1978; Szlavecz 1985) and the importance of earthworm middens for Collembola (Loksa 1978), Oribatida (Bayoumi 1978) and Enchytraeidae (Dózsa-Farkas 1978) was emphasized. Dózsa-Farkas (1978) found that in forest soil two species of Enchytraeidae (*Stercutus niveus* and *Fridericia galba*) preferred earthworm middens while the abundance of four other species showed no significant difference between earthworm middens and the non-midden soil. Eight of 15 collembolan species from the same study site which were selected for statistical analysis significantly preferred earthworm middens. The other seven species showed no preference or were even less abundant in middens (Loksa 1978). Out of ten oribatid mite species which were selected for analysis of variance only two small Oppiidae (*Oppia ornata* and *Oppiella obsoleta*) significantly preferred earthworm middens (Bayoumi 1978).

The effect of midden formation on nematode populations is controversial. While Hamilton et al. (1988) found that nematode densities decreased significantly in the upper layers of sludge-amended soil microcosms in the presence of *L. terrestris*, Russom et al. (1993) noticed that in casts of the earthworm *Agrotoreutus nyongi* there were more nematodes than in soil. In microcosm experiments Yeates (1981) found nematode populations from New Zealand pastures to be reduced by 37–66 % in the presence of earthworms, while some plant parasitic genera (*Ditylenchus* and *Paratylenchus*) showed marked increases.

In this study we investigated the significance of *L. terrestris* middens for soil microflora, micro- and mesofauna in a beechwood (*Fagus sylvatica* L.) on limestone (Göttinger Wald, Lower Saxony, Germany). The parent rock at this site is limestone which is covered with a rendzina soil with the mull humus form. The deep-burrowing anecic earthworm *L. terrestris* lives in permanent burrows branching near the soil surface. With an average of about 30 per square meter middens have been assumed to be important microhabitats of the forest floor in the Göttinger Wald (Schaefer 1990). We therefore investigated the density and species composition of major soil animal groups including Gamasina, Uropodina, Collembola, Oribatida and Nematoda in middens of *L. terrestris* and the surrounding soil. Also, abiotic and microbial parameters were measured. We hypothesized that due to an increased microbial biomass in earthworm middens the density of the microbivorous meso- and microfauna will also be higher which is based on the assumption that bottom-up factors dominate in controlling soil organisms. Furthermore, we expected some species to specifically inhabit middens due to a unique combination of abiotic and biotic factors in this microhabitat.

Materials and Methods

Study site

The study was carried out in the Göttinger Wald, a c. 120 yr old beech forest located on a limestone plateau east of Göttingen (Lower Saxony, Germany). The soil type varies considerably but was of the rendzina-type in the area studied with an average soil pH of 5.3. The soil fauna of this site has been intensively investigated (cf. Schaefer 1990).

Sampling

In September 1994 soil samples were taken (∅ 5 cm) to a depth of 3 cm from middens of *Lumbricus terrestris* L. and from control mineral soil at c. 20 cm distance from middens. We focussed on the effect of *L. terrestris* on the fauna living in the mineral soil since in the forest studied most soil animals inhabit the upper mineral soil. Therefore, the litter material was removed from the soil surface prior to sampling. Six replicates of midden material and of the surrounding non-midden soil were taken. Each replicate consisted of six pooled (carefully mixed by hand) samples from midden and non-midden soil. The material was subdivided for microbial analysis and animal extraction.

Soil mesofauna (Gamasina, Uropodina, Collembola, Oribatida) was extracted by heat from 100 g fresh weight of soil (Macfadyen 1961; Schauermann 1982). Individuals were determined to species level and counted, and the average density on a square meter basis was calculated.

Nematodes were extracted from 20 g fresh weight of soil from each of the mixed samples on the day of collection using Baermann funnels in a modified O'Connor wet extraction apparatus (Alphei 1995). Subsequently, nematodes were killed by heat and fixed in 4 % formaldehyde solution. Total numbers of nematodes were counted under a dissection microscope. Out of each sample, 100 specimens were picked at random, which were determined to genus level, except for rhabditid and tylenchid juveniles, which were identified to family level. Nematodes were classified into six trophic groups (bacterial feeders, fungal feeders, root hair feeders, omnivores, plant parasites and predators) according to Yeates et al. (1993). Individual fresh weights were calculated using the formula of Andrássy (1956). Dry weight of nematodes was calculated as 22.5 % of fresh weight (cf. Sohlenius 1979; Buecher & Hansen 1971).

Microbial biomass carbon (SIR-method, Anderson & Domsch 1978) and basal respiration were measured from subsamples of soil using an automated O_2-microcompensation apparatus (Scheu 1992). From these data the specific respiration was calculated (qO_2; Maraun & Scheu 1996). Total C and N contents of the soil were determined using an elemental analyser (Carlo Erba, Milan, Italy).

Statistical analysis

Data on carbon and nitrogen content, C/N ratio, microbial biomass, basal respiration, specific respiration and animal density in earthworm middens and non-midden soil were analysed by t-tests (SAS Institute 1995). Prior to the t-tests data were log-transformed to improve normality.

To analyse the response of different taxa or groups of Gamasina, Uropodina, Oribatida, Collembola and Nematoda single-factor multivariate analysis of variance (MANOVA, Roy's greatest root) was used (cf. Scheiner 1993). For these analyses species were pooled to supraspecific taxa in Gamasina, Uropodina, Oribatida and Collembola. Nematode species were grouped according to functional similarity (Yeates et al. 1993). Taxa or groups which, after pooling, contributed less than 5 % to the density of Gamasina, Uropodina, Oribatida, Collembola or Nematoda were excluded from the analysis.

To analyse the response at the species (Gamasina, Uropodina, Oribatida, Collembola), genus or family level (Nematoda) separate principal component analyses (PCA) were carried out for Gamasida (Gamasina plus Uropodina), Collembola, Oribatida and Nematoda. In these analyses midden and non-midden soil was coded by dummy variables and included using the passive analysis procedure in CANOCO (Ter Braak 1988; Jongman et al. 1995), i.e. variables did not contribute to the ordination. Only species which were found in at least three separate samples were included in the analyses. In addition, a PCA including all the supraspecific taxa or groups of Uropodina, Oribatida, Collembola and Nematoda was carried out to depict the interrelationships between these groups. Since, as indicated by MANOVA, there was no differential response of the taxa of Gamasina to midden and non-midden soil, Gamasina was included as a single group in the PCA. Prior to the analyses data were log-transformed.

Results

Carbon and nitrogen

Carbon content in middens considerably exceeded that in non-midden soil (+45 %, Table 1). Although the nitrogen content was also significantly greater, the difference was less pronounced (+17 %). Also, the C-to-N ratio in middens exceeded that in non-midden soil (+22 %).

Table 1. Abiotic and microbial properties and density and biomass of soil animals in middens of *Lumbricus terrestris* and in non-midden soil. Values of animal densities and nematode biomass are back-transformed means of log-transformed data

	Midden	Non-midden	t-value
Carbon content (%)	11.3	7.8	49.8***
Nitrogen content (%)	0.68	0.58	8.2*
C/N ratio	16.6	13.6	26.8***
Microbial biomass (mgC_{mic}/g dry wt)	2.3	1.4	53.0***
Basal respiration (μlO_2/g dry wt*h)	10.5	4.9	47.0***
Specific respiration ($\mu lO_2/mgC_{mic}$*h)	4.5	3.3	9.4*
Gamasina (Ind/m^2)	1859	1070	8.5*
Uropodina (Ind/m^2)	1160	100	5.4*
Collembola (Ind/m^2)	52481	32174	5.9*
Oribatida (Ind/m^2)	6344	6953	0.3 ns
Nematoda (Ind/g dry wt soil)	26.4	20.3	3.2 ns
Nematoda (µg dry wt/g dry wt soil)	5.9	2.0	8.3*

*** $P<0.001$; * $P<0.05$; ns: not significant

Microflora

Corresponding to the greater content of carbon and nitrogen, microbial biomass (+64 %) and basal respiration (+114 %) were significantly increased in midden soil (Table 1). The more pronounced increase in basal respiration compared to microbial biomass resulted in a higher specific respiration in midden material (+36 %) than in non-midden soil.

Meso- and Microfauna

The density of Gamasina in middens significantly exceeded that in non-midden soil (+74 %, Table 1). There was no differential response of supraspecific taxa of Gamasina (Eviphidoidea, Phytoseioidea, Ascoidea and Eugamasoidea) as indicated by MANOVA ($F=3.5$, $P=0.1$). However, principal component analysis (PCA) indicated that certain species of Gamasina preferrentially occurred in middens (Fig. 1a). Species of the Parasitidae (*Leptogamasus suecicus, Lysigamasus lapponicus, L. runcatellus, Pergamasus septentrionalis*) and Ascoidea (*Leitneria granulata*) and *Veigaia nemorensis* were more abundant in middens than in non-midden soil. In contrast, only few species (*Lysigamasus solitarius, Macrholaspis dentatus* and *Veigaia agilis*) preferentially colonized non-midden soil. The species associated with middens were generally more abundant than those of the mineral soil.

The abundance of Uropodina in middens exceeded that in non-midden soil by a factor of 11.6 (Table 1). MANOVA and PCA indicated that groups and species of Uropodina differed in respect to colonization of middens ($F=126.6$, $P<0.001$, MANOVA). While Urodinychidae (*Dinychus perforatus*) and Trachytidae (mainly *Trachytes aegrota*) were closely associated with middens, this was less pronounced for Uropodidae (*Uropoda willmanni, U. athiasae* and *U. cassidea*; Fig. 1a and 2).

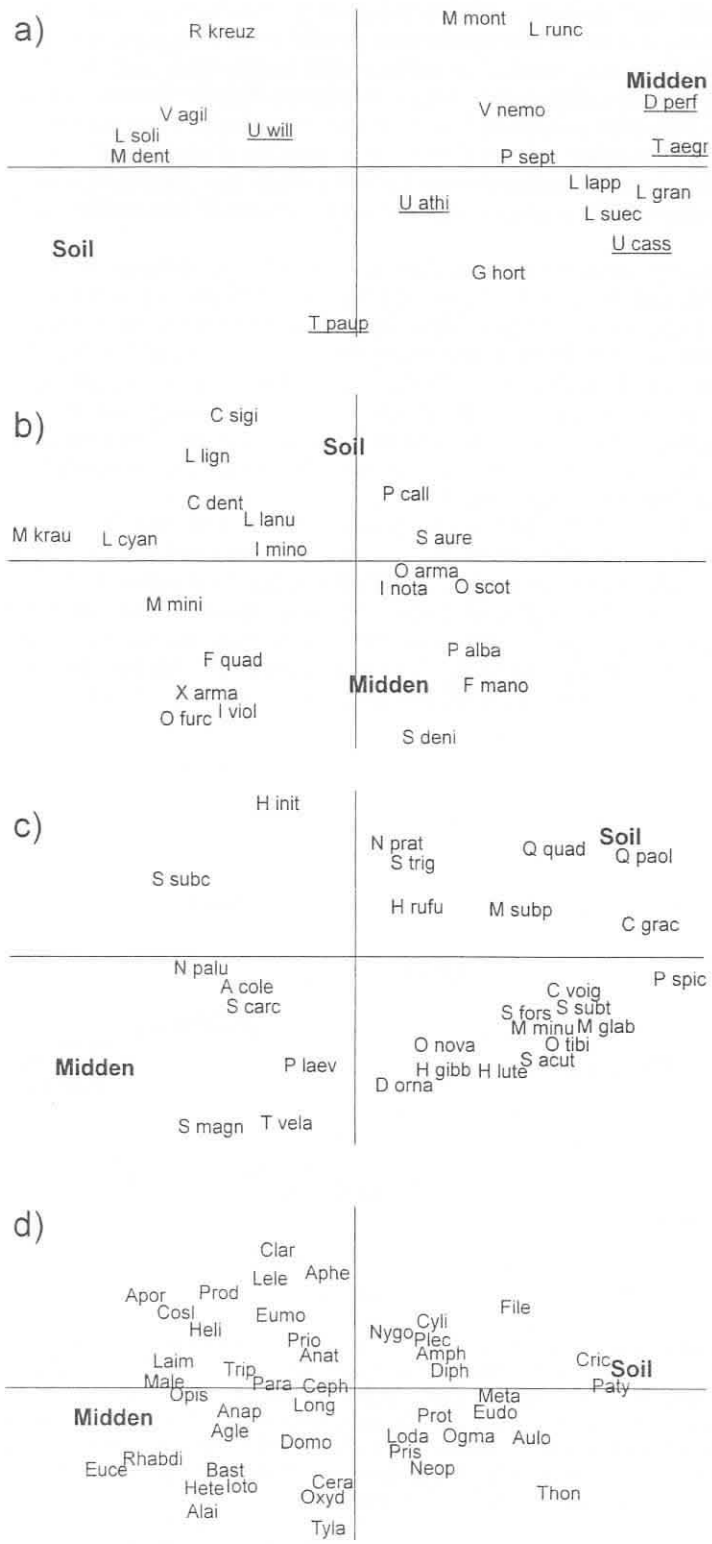

Fig. 1. PCA plot of species of (a) Gamasina and Uropodina (underlined), (b) Collembola, (c) Oribatida and (d) species and genera of Nematoda in middens (midden) and non-midden soil (soil). Eigenvalues of axis 1 and 2 are 0.37 and 0.21 (a), 0.24 and 0.16 (b), 0.26 and 0.18 (c) 0.29 and 0.17 (d), respectively. Full species, genera and family names are given in the Appendix

Density of Collembola in middens exceeded that in non-midden soil by a factor of 1.6 (Table 1). MANOVA indicated that subgroups of Collembola differentially responded to the presence of middens. While the density of Isotomidae was greater, that of Hypogastruridae, Entomobryidae and Onychiuridae was similar in midden and non-midden soil ($F = 5.6$, $P < 0.05$, Fig. 2). PCA with data on collembolan species confirmed that the density of Isotomidae (*Isotoma violacea, Folsomia quadrioculata, Folsomia manolachei*) was increased in middens but also showed that other species (*Onychiurus furcifer, Pseudosinella alba, Stenaphorurella denisi*) were closely associated with middens. Only two species (*Lepidocyrtus lanuginosus* and *Ceratophysella sigillata*) preferrentially colonized non-midden soil (Fig. 1b).

In contrast to the other groups studied Oribatida were less abundant in middens as compared to non-midden soil although the difference was not significant (Table 1). MANOVA confirmed that most oribatid mite taxa were more abundant in non-midden soil (Brachychthonidae, Oppiidae and Poronota); only Phthiracaridae appeared to be associated with middens ($F = 10.3$, $P < 0.01$, Fig. 2). According to PCA the genus *Quadroppia* (*Q. paoli* and *Q. quadricarinata)* and the species *Medioppia subpectinata, Ceratozetes gracilis* and *Poecilochthonius spiciger* were closely associated with non-midden soil whereas *Steganacarus magnus, Nothrus palustris, Tectocepheus velatus, Achipteria coleoptrata* and *Suctobelbella carcharodon* were more abundant in middens (Fig. 1c).

Free-living nematodes were more abundant in middens than in non-midden soil (+31.5 %), however, the difference was not significant (Table 1). In contrast, the biomass of nematodes in middens significantly exceeded that in non-midden soil on average by a factor of 3. The difference was mainly due to bacterial feeding and omnivorous species exceeding the biomass in non-midden soil by factors of 2.4 and 7.5, respectively. However, overall, there was no significant difference in nematode feeding groups between midden and non-midden soil, as indicated by MANOVA ($F = 1.7$, $P = 0.34$ for density and $F = 3.2$, $P = 0.18$ for biomass).

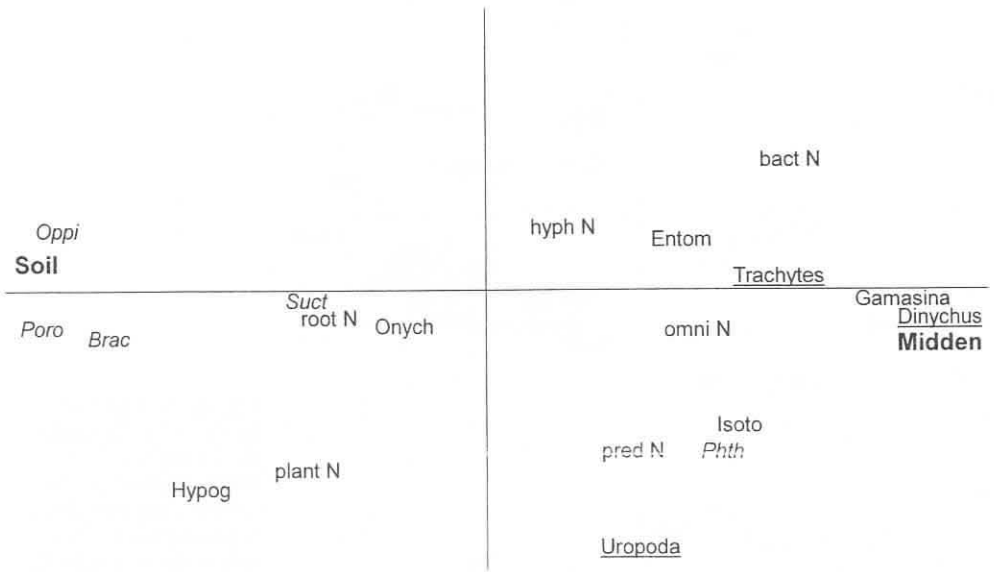

Fig. 2. PCA plot of Gamasina and taxa or sub-groups of Uropodina, Collembola, Oribatida and Nematoda in middens (midden) and non-midden soil (soil). Entom, Entomobryidae; Hypog, Hypogastruridae; Onych, Onychiuridae; Isoto, Isotomidae; Brac, Brachychthonidae, Oppi, Oppiidae; Phth, Phthiracaridae; Poro, Poronota, Suct, Suctobelbidae, bact N, bacterial feeding nematodes; hyph N, hyphal feeding nematodes; omni N, omnivorous nematodes; plant N, plant feeding nematodes; pred N, predacious nematodes; root N, root feeding nematodes. Uropodina are underlined; Oribatid mite groups are in italics. Eigenvalues of axis 1 and 2 are 0.45 and 0.21, respectively

However, PCA indicated that the bacterial feeding *Eucephalobus* and *Rhabditis* juveniles were closely associated with middens, while *Aulolaimus* and *Metateratocephalus* were more abundant in non-midden soil. In addition, the plant parasitic genera *Criconema* and *Paratylenchus* appeared to flourish in non-midden soil. Remarkably, the root hair feeding *Filenchus* and *Malenchus* responded differently. *Malenchus* was more abundant in middens, while *Filenchus* was associated with non-midden soil. Overall, however, the majority of nematode genera responded little to the presence of middens (Fig. 1d). Generally, the variance accounted for by the first two PCA axes was in a similar range for each of the groups studied (Gamasida 58.0 %, Oribatida 44.5 %, Collembola 40.6 %, Nematoda 46.0 %).

Response of the community

Principal component analysis of mesofaunal groups and Nematoda confirmed the results of the separate MANOVAs and PCAs. While Gamasina, Trachytidae (Uropodina) and Urodinychidae (Uropodina), Isotomidae (Collembola), Phthiracaridae (Oribatida) and bacterial feeding and omnivorous nematodes were associated with middens, Brachychthonidae, Oppiidae, Poronota (all Oribatida) were associated with non-midden soil (Fig. 2). Generally, the first two PCA axes accounted for 65.9 % of the variance in species data of the community of Gamasida, Oribatida, Collembola and Nematoda.

Discussion

Middens of *Lumbricus terrestris* may be favourable habitats for certain animal taxa and therefore contribute to microarthropod diversity, however midden formation may also reduce the density and diversity of microarthropods due to disturbance and habitat destruction, e.g. litter removal and bioturbation (Brown 1995). In mull soils like the 'Göttinger Wald' the influence of large saprophagous animals (e.g. earthworms, diplopods, isopods) on soil structure and other abiotic factors is much stronger than in moder or raw humus soil forests where macrofaunal activity is low. In this forest, for example, *L. terrestris* forms up to 35 middens per square metre. Therefore, earthworms, particularly *L. terrestris*, are potentially important agents in forming the habitat of other soil animals. To determine whether the presence of middens affects the density and diversity of other soil animals we compared abiotic factors, microbial parameters and the density and species composition of the mesofauna and nematodes in midden and non-midden soil.

Carbon and nitrogen content and microbial parameters (microbial biomass, basal respiration, specific respiration) in middens were significantly greater than in non-midden soil whereas soil density was lower in middens (data not presented). The meso- and microfauna differentially responded to the presence of middens.

The density of Collembola was greater in middens than in non-midden soil. Higher density of Collembola in middens was due to Isotomidae (*Isotoma violacea, Folsomia quadrioculata, Folsomia manolachei*) and *Onychiurus furcifer, Stenaphorurella denisi* and *Pseudosinella alba*. High density of two species of the genus *Folsomia* in middens of *L. terrestris* has also been reported by Loksa (1978). Isotomidae are ubiquitous generalists that may have benefited from enhanced food supply (microbial biomass) in middens. Isotomidae may also have benefited from the high nematode biomass in middens since there is increasing evidence that Isotomidae (especially *Folsomia*) feed on nematodes (Walter 1987; Gilmore & Potter 1993; Lee & Widden 1996). Of the Tullbergiinae large species like *Paratullbergia callipygos* and *Stenaphorurella denisi* were more abundant in middens whereas small species like *Mesaphorura krausbaueri* achieved greatest numbers in non-midden soil. In contrast to Isotomidae, species of the genus *Lepidocyrtus* (*L. cyaneus, L. lanuginosus* and *L. lignorum*) were more abundant in non-midden soil. This is surprising since these species prefer to colonize habitats rich in organic matter and middens were richer in carbon compared to non-midden soil. Possibly, *Lepidocyrtus* species were detrimentally affected by disturbances caused by midden formation.

In contrast to the other animal groups investigated in this study, the density of oribatid mites in middens did not exceed that in non-midden soil; in fact, the density was somewhat lower in midden as compared to non-midden soil. This may reflect the sensitivity of oribatid mite species to disturbances (Norton & Palmer 1991). In contrast to other mite taxa and also to most other mesofauna species, the development of oribatid mite species is slow (Luxton 1981; Norton & Palmer 1991), therefore disturbances due to removal of litter and production of casts may detrimentally affect oribatid mite populations. Particularly small oribatid mite species like Brachychthonidae (*Poecilochthonius spiciger*) and some Oppiidae (*Quadroppia quadricarinata, Q. paolii, Medioppia subpectinata*) and species of the group Poronota (*Chamobates voigtsi, Ceratozetes gracilis*) appear to be sensitive to disturbances whereas Phthiracaridae (*Steganacarus magnus, Phthiracarus leavigatus*) appear to be more resistant. Brachychthonidae are known to reach high density and diversity in raw humus and moder soils whereas in mull soils only few species of Brachychthonidae are present at low density. Mull soils are characterized by high earthworm activities with middens being the most disturbed areas. Presumably, earthworm activities in mull soils detrimentally affect the development of brachychthonids (Brown 1995; McLean & Parkinson 1998). Brachychthonidae only lay one or two eggs per brood (Forsslund 1942, 1957) and develop slowly from the juvenile to the adult stage (Travé et al. 1996). The same may be true for Oppiidae and Poronota of which most species had low density in middens. Only a few parthenogenetic oribatid species like *Tectocepheus velatus, Oppiella nova* and *Punctoribates punctum* frequently occur in disturbed sites like fields or at sites in an early successional stage (Scheu & Schulz 1996).

Earthworms may affect soil nematode populations directly by ingesting and digesting nematodes when feeding on soil and litter (Dash et al. 1980; Piearce & Phillips 1980) or indirectly, by modifying habitat characteristics like soil structure, water regime and nutrient cycling (Yeates 1981). Results of this study indicate, however, that the community of soil nematodes was only little, if at all, affected by midden formation. The total number of free-living nematodes tended to be higher in earthworm middens, however the difference was not significant. In other studies the presence of earthworms was found to markedly reduce total numbers of nematodes in laboratory systems (Hyvönen et al. 1994; Hamilton et al. 1988) as well as in the field (Yeates 1981). In contrast to most nematode genera, the biomass of bacterial feeding nematodes was greater in middens, which may have resulted from an increased amount of food resources, i.e. microbial biomass. Of the bacterial feeders, the increase in density of Rhabditidae and *Eucephalobus* was most pronounced. Both groups are known to be colonizers (Bongers 1990) and may have benefited from bacterial populations on decomposing litter particles incorporated in middens. In contrast, the plant parasitic genera *Criconema* and *Paratylenchus* were more abundant in non-midden soil. This is in accordance with results of Roessner (1986) who found plant parasitic nematodes to be reduced in the faeces of *L. terrestris*. Senapati (1992) also reported lower numbers of plant parasitic nematodes in the presence of a tropical earthworm species (*Lampito mauritii*). The most abundant root hair feeders were *Filenchus* and *Malenchus* which are assumed to feed on similar resources (Yeates et al. 1993). However, in the present study *Filenchus* was more abundant in non-midden soil whereas *Malenchus* was associated with middens indicating niche differentiation. As assumed by Magnusson (1983 a,b) *Malenchus* feeds on fungal hyphae which may have been more abundant in middens.

Gamasina were generally more abundant in middens than in non-midden soil. However, Eviphidoidea, Phytoseioidea, Ascoidea and Eugamasoidea responded little to the presence of middens, indicating little niche separation. In contrast, the response of the genera *Lysigamasus, Leptogamasus, Pergamasus* and *Veigaia nemorensis* to the presence of middens was more pronounced. These large species are known to prey mainly on Collembola and to a lesser extent on nematodes (Karg 1989; Koehler 1997). Presumably they benefited from the high abundance of Collembola (mainly Isotomidae) and from the high biomass of nematodes in middens. Therefore, middens appear to be important microhabitats for certain Gamasina, especially Parasitidae and Veigaiaidae.

Like Gamasina, Uropodina were more abundant in middens than in non-midden soil. One species, *Dinychus perforatus*, was only found in middens, while species of the genera *Uropoda* and *Trachytes* were differentially affected by the presence of middens. In contrast to the assumption of Karg (1963) that Uropodina feed on fungi and algae, recent studies have shown that they are predators feeding on nematodes, insect larvae and enchytraeids with nematodes being preferred (Karg 1989; Koehler 1997). Due to their slow movement in the soil and litter matrix Uropodina presumably are unable to feed on Collembola. Therefore, Uropodina presumably benefited from the high nematode biomass in middens. Especially members of the taxon Urodinychidae are assumed to feed preferentially on nematodes (Athias-Binche 1981).

In conclusion, most species of Gamasina and Uropodina (*Dinychus perforatus* and *Trachytes aegrota*), bacterial feeding and omnivorous Nematoda and some groups of Collembola (mainly Isotomidae) benefited from the presence of middens, supporting the view that earthworm middens form important microhabitats in the forest studied. In contrast, most oribatid mites (Brachychthonidae, Oppiidae, Suctobelbidae, Poronota) were negatively affected by the presence of middens indicating that oribatid mites are most sensitive to disturbances. Overall, the results confirm the assumption of Brown (1995) that earthworm middens are beneficial for most soil animals.

Unfortunately, in most cases the reasons for the flourishing of the soil animals in middens remain speculative. However, most taxa presumably benefited from an increased amount of food resources in middens, supporting the view that bottom-up forces dominate in decomposer communities (Hairston et al. 1960; Scheu & Schaefer 1998).

It has been speculated that microhabitats like earthworm middens may contribute to the high diversity of soil animals due to an increase in niche diversity (Anderson 1975; Schaefer 1991; Giller 1996). Results of the present study do not support this view. Almost all species which occurred in middens were also present in non-midden soil. Therefore, niche differentiation appears to be insufficient to explain the high diversity of soil invertebrates as has been assumed previously for oribatid mites (Maraun et al. 1998).

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Appendix. Species list of Gamasina, Uropodina, Collembola, Oribatida and genera/family list of Nematoda with abbreviations used in the figures.

Gamasina

Geholaspis hortorum (Berlese, 1904) [G hort], *Leitneria granulata* (Halbert, 1923) [L gran], *Leptogamasus suecicus* (Trägardh, 1936) [L suec], *Lysigamasus lapponicus* Trägardh, 1910 [L lapp], *Lysigamasus runcatellus* (Berlese, 1903) [L runc], *Lysigamasus solitarius* Karg, 1968 [L soli], *Macrholaspis dentatus* Evans & Browning 1956 [M dent], *Macrocheles montanus* (Willmann, 1951) [M mont], *Pergamasus septentrionalis* Oudemans, 1902 [P sept], *Rhodacarellus kreuzi* Karg, 1965 [R kreu], *Veigaia agilis* (Berlese, 1916) [V agil], *Veigaia nemorensis* (C.L. Koch, 1839) [V nemo].

Uropodina

Dinychus perforatus Kramer, 1882 [D perf], *Trachytes aegrota* (C.L. Koch, 1841) [T aegr], *Trachytes pauperior* Berlese 1914 [T paup], *Uropoda athiasae* Hirschmann & Zirngiebl-Nicol, 1969 [U athi], *Uropoda cassidea* (Hermann, 1804) [U cass], *Uropoda willmanni* Hirschmann & Zirngiebl-Nicol, 1969 [U will].

Collembola

Ceratophysella denticulata (Bagnall, 1941) [C dent], *Ceratophysella sigillata* (Uzel, 1891) [C sigi], *Folsomia manolachei* Bagnall 1939 [F mano], *Folsomia quadrioculata* (Tullberg, 1871) [F quad], *Isotomiella minor* (Schaeffer, 1896) [I mino], *Isotoma notabilis* (Schaeffer, 1896) [I nota], *Isotoma viridis* Bourlet, 1839 [I viri], *Isotoma violacea* Tullberg, 1876 [I viol], *Lepidocyrtus cyaneus* Tullberg, 1871 [L cyan], *Lepidocyrtus lanuginosus* (Gmelin, 1788) [L lanu], *Lepidocyrtus lignorum* Fabricius 1775 [L lign], *Megalothorax minimus* Willem, 1900 [M mini], *Mesaphorura* cf. *krausbaueri* Börner, 1901 [M krau], *Onychiurus armatus* (Tullberg, 1869) [O arma], *Onychiurus furcifer* (Börner, 1901) [O furc], *Onychiurus scotarius* Gisin, 1954 [O scot], *Paratullbergia callipygos* (Börner, 1902) [P call], *Pseudosinella alba* (Packard, 1873) [P alba], *Sminthurinus aureus* (Lubbock, 1862) [S aure], *Stenaphorurella denisi* (Bagnall, 1935) [S deni], *Xenyllodes armatus* Axelson, 1903 [X arma].

Oribatida

Achipteria coleoptrata (Linnaeus, 1758) [A cole], *Ceratozetes gracilis* (Michael, 1884) [C grac], *Chamobates voigtsi* (Oudemans, 1902) [C voig], *Dissorhina ornata* (Oudemans, 1900) [D orna], *Hemileius initialis* (Berlese, 1908) [H init], *Hermannia gibba* (C.L. Koch, 1839) [H gibb], *Hypochthonius luteus* Oudemans, 1917 [H lute], *Hypochthonius rufulus* C.L. Koch, 1835 [H rufu], *Microppia minus* (Paoli, 1908) [M minu], *Medioppia subpectinata* (Oudemans, 1900) [M subp], *Multioppia glabra* (Mihelcic, 1955) [M glab], *Nothrus palustris* C.L. Koch, 1839 [N palu], *Nothrus pratensis* Sellnick, 1928 [N prat], *Oppiella nova* (Oudemans, 1902) [O nova], *Oribatula tibialis* (Nicolet, 1855) [O tibi], *Phthiracarus laevigatus* (C.L. Koch, 1844) [P laev], *Poecilochthonius spiciger* (Berlese, 1910) [P spic], *Quadroppia paolii* (Paoli, 1908) [Q paol], *Quadroppia quadricarinata* (Michael, 1885) [Q quad], *Steganacarus magnus* (Nicolet, 1855) [S magn], *Suctobelbella acutidens* (Forsslund, 1841) [S acut], *Suctobelbella carcharodon* (Moritz, 1966) [S carc], *Suctobelbella forsslundi* (Strenzke, 1950) [S fors], *Suctobelbella subcornigera* (Forsslund, 1941) [S subc], *Suctobelbella subtrigona* (Oudemans, 1900) [S subt], *Suctobelba trigona* (Michael, 1888) [S trig], *Tectocepheus velatus* (Michael, 1880) [T vela].

Nematoda

Aglenchus Andrássy, 1954 [Agle], *Alaimus* de Man, 1880 [Alai], *Amphidelus* Thorne, 1939 [Amph], *Anaplectus* de Coninck & Schuurmans Stekhoven, 1933 [Anap], *Anatonchus* (Cobb, 1916) [Anat], *Aphelenchoides* Fischer, 1894 [Aphe], *Aporcelaimellus* Heyns, 1965 [Apor], *Aulolaimus* de Man, 1880 [Aulo], *Bastiania* de Man, 1876 [Bast], *Cephalobus* Bastian, 1865 [Ceph], *Ceratoplectus* Andrássy, 1984 [Cera], *Clarkus* Jairajpuri, 1970 [Clar], *Coslenchus* Siddiqi, 1978 [Cosl], *Criconema* Hofmaenner & Menzel, 1914 [Cric], *Cylindrolaimus* de Man, 1880 [Cyli], *Diphterophora* de Man, 1880 [Diph], *Domorganus* Goodey, 1947 [Domo], *Eucephalobus* Steiner, 1936 [Euce], *Eudorylaimus* Andrássy, 1959 [Eudo], *Eumonhystera* Andrássy, 1981 [Eumo], *Filenchus* Andrássy, 1954 [File], *Helicotylenchus* Steiner, 1945 [Heli], *Heterocephalobus* Brzeski, 1960 [Hete], *Iotonus* (Cobb, 1916) [Ioto], *Laimydorus* Siddiqi, 1969 [Laim], *Lelenchus* Andrássy, 1954 [Lele], *Longidorella* Thorne, 1939 [Loda], *Longidorus* Micoletzky, 1922 [Long], *Malenchus* Andrássy, 1968 [Male], *Metateratocephalus* Eroshenko, 1973 [Meta], *Neopsilenchus* Thorne & Malek, 1968 [Neop], *Nygolaimus* Thorne, 1930 [Nygo], *Ogma* Southern, 1914 [Ogma], *Opisthodorylaimus* Ahmad & Jairajpuri, 1982 [Opis], *Oxydirus* Thorne, 1939 [Oxyd], *Paramphidelus* Andrássy, 1977 [Para], *Paratylenchus* Micoletzky, 1922 [Paty], *Plectus* Bastian, 1865 [Plec], *Prionchulus* Wu & Hoeppli, 1929 [Prio], *Prismatolaimus* de Man, 1880 [Pris], *Prodorylaimus* Andrássy, 1959 [Prod], *Protorhabditis* Osche, 1956 [Prot], *Rhabditidae* Oerley, 1880 [Rhabdi], *Thonus* Thorne, 1974 [Thon], *Tripyla* Bastian, 1865 [Trip], *Tylencholaimus* de Man, 1876 [Tyla].